24

Dietary Fatty Acids and Minerals

Henry C. Lukaski
United States Department of Agriculture, Grand Forks, North Dakota

INTRODUCTION

The absorption of dietary minerals is determined by the nutritional needs of the organism, by the amount present in the diet, and by factors influencing the bioavailability and utilization of the mineral. Whereas nutritional needs tend to modulate homeostatic mechanisms of absorption, the bioavailability of minerals is principally influenced by exogenous factors. Factors influencing mineral bioavailability can be grouped as to the site at which they occur and include luminal, mucosal, and postabsorptive events (Rosenberg and Solomons, 1984). Luminal events refer to the dissociation of the mineral from the chemical matrix with which it was associated in the food and possible interactions with factors that may enhance or reduce its solubility. Mucosal actions include uptake of minerals at the mucosal membrane which may or may not include receptors. Postabsorptive transport of minerals away from the intestinal epithelium to body tissues and organs involves the participation of binding or transport proteins. Each of these factors or processes depends on nutrients and chemical compounds in the diet that directly or indirectly affect absorption and utilization of minerals. Other factors, such as enteral recycling and hormonal influences, may also play a role.

Nutritionists seek to identify dietary factors that affect mineral bioavailability and to quantify the beneficial or detrimental effects of these factors on mineral absorption and utilization. This basic information is needed to develop recommendations for intakes of essential minerals for various groups in the population.

Many dietary components have been shown to influence mineral bioavailability in animals and humans (Solomons and Rosenberg, 1984). Some of these include protein, carbohydrate, fiber, organic acids, other minerals, and drugs. One dietary component, fat or fatty acids, has received minimal attention. One reason may be that there is little in vitro physico-chemical evidence to suggest that fatty acids will bind minerals, because stability constants are negligible or nonexistent (Sillen and Martell, 1964; Perrin, 1979; Martell and Smith, 1982). However, because dietary fat represents a significant fraction of daily energy intake in the United States, with estimates ranging from 30 to 40% of energy intake (Life Sciences Research Office, 1989), and because in vivo physiological interactions between fatty acids and minerals have been reported (Simpson and Peters, 1987a, 1987b; Simpson et al., 1988),

there is increasing interest in examining the effects of dietary fatty acids on the bioavailability of minerals.

The purpose of this chapter is to summarize research findings on the effects of dietary fat on the bioavailability of some essential minerals, including calcium and magnesium and the trace minerals, copper, zinc, and iron. This chapter also will integrate the experimental findings on bioavailability with current understanding of the mechanisms of mineral absorption.

METHODOLOGY AND CONCEPTS

Two general experimental approaches have been used to examine the effects of dietary fat on mineral bioavailability. Chemical balance methods, defined as the difference between intake of an element and the sum of urinary, fecal, and surface losses of an element, have been used in animal and human studies to determine the enhancement or inhibition of specific fatty acids and triglycerides on mineral balance. If chemical balance is reduced, that is, fecal losses are increased, the fat is considered to affect mineral bioavailability deleteriously.

Another technique involves the use of an isotope of the element under study to assess in vivo mineral metabolism. The isotope may be either added to a test meal (e.g., extrinsic label) or incorporated into a test food or component of a meal (e.g., intrinsic label). If a radioisotope is used, the absorption and retention are calculated by using serial determinations of the remaining radioactivity in the animal or human subject after consumption of the test meal. These values are used to estimate the biological half-life of the tracer, and hence the mineral. When a stable isotope is used, fecal samples are analyzed for isotope content. Fecal loss of the tracer determined over time is an index of relative bioavailability.

CALCIUM

The problem of determining calcium requirements of humans remains after more than 75 years of research despite the recognition that calcium is essential for proper bone formation. One aspect of this research has been the study of factors that influence calcium absorption and retention (Irwin and Kienholz, 1973). The objective is to determine the effect of dietary components on the availability of calcium from foods. Fat is among the dietary components studied.

Animal Studies

The influence of dietary fat on apparent calcium absorption, defined as the difference between calcium intake and fecal calcium losses, in laboratory animals has received considerable study with somewhat conflicting results, probably because of differences in age or development of the animals and dietary conditions (Table 1). In many of the studies, experimental conditions were optimized to find an effect of dietary fat on calcium utilization (e.g., low dietary calcium); low-fat or fat-free control diets also were used. Some investigators found that addition of dietary fat increased either calcium absorption or utilization of calcium in bone in comparison to the low-fat or fat-free control diet (McDoughall, 1938; Jones, 1940; Knudson and Floody, 1940). However, as the fat intake increased in excess of 10% of daily energy intake, calcium absorption and the bone calcium content began to decrease (Knudson and Floody, 1940). Other investigators reported that fats have an inhibitory effect on calcium absorption and utilization (Smith and Spector, 1940; French and Elliott, 1943; Calverley and Kennedy, 1949; Kane, et al., 1949; Beadles et al., 1951; Swell et al., 1956). These data provide no clear discrimination between the type of fat (saturated vs unsaturated) on the observed effects of either calcium absorption or utilization. It does appear, however, that increasing the fat content, regardless of the type, may decrease dietary calcium absorption and utilization in the rat.

These investigations were complemented by the recognition that dietary calcium per se may influence dietary fat absorption. The presence of ionized calcium in the intestine determines the extent

TABLE 1 Effects of Dietary Fats on Calcium (Ca) Absorption, Retention, and Utilization in Rats

Reference	Diet	Finding
McDoughall (1938)	11% lard or olive oil, vitamin D deficient	Prevented rickets
Knudson and Floody (1940)	5% cotton seed oil, vitamin D deficient; 10–20% cotton-seed oil, vitamin D deficient	Increased bone calcification
Jones (1940)	10% lard, vitamin D deficient	Increased ash
Smith and Spector (1940)	5% mineral oil	Reduced bone calcification
French and Elliott (1943)	5–45% oleo oil	Ca retention decreased as fat intake increased
Calverly and Kennedy (1949)	5% coconut oil or cotton seed oil	Decreased Ca retention
	5% peanut oil	No effect
Kane et al. (1949)	1–21% corn oil	Decreased Ca absorption
Beadles et al. (1951)	20% cocoa butter	Decreased Ca retention
	20% lard	No effect
Swell et al. (1956)	20% oleic acid, 20% palmitic acid	50% loss of Ca
Nordin (1961)	Low-Ca diet, 20% tripalmitin or tristearin	Reduced ^{47}Ca absorption and retention
Tadayyon and Lutwak (1969)	25% tripalmitin or tristearin	Decreased Ca absorption and retention
Kaup et al. (1990)	0.25 or 1.0% Ca 5 or 20% butterfat	Increased butterfat absorption only in mature rats

of soap formation, although the amount ultimately excreted in the feces depends on the solubility of the soap formed, which is inversely related to chain length and degree of unsaturation. When a diet containing a relatively high calcium intake (60–70 mg/day) was fed to rats, the utilization of oleate, palmitate, and stearate soaps was found to be 90, 38, and 25%, respectively. Conversely, when a relatively low-calcium diet was used (13.5–41.4 mg/day), the absorption of palmitate and stearate was increased to 65 and 45%, respectively (Boyd et al., 1932). The fact that oleate soaps were used preferentially to the soaps of the saturated fatty acids indicates that the melting point is an important factor influencing the absorption of fats and their soaps.

More recent animal studies in which calcium intake was controlled have also attempted to reassess the effects of dietary fats on calcium utilization. Tadayyon and Lutwak (1969) reported that supplementation of a fat-free diet for 2 weeks with 25% tripalmitin or tristearin depressed calcium absorption. The calcium content of the femur in rats receiving 25% triolein or 5% fat as triolean, tripalmitin, or tristearin was greater than that of the animals receiving the fat-free diet, and this was greater that those fed 25% tripalmitin or tristearin. The femur calcium content increased when the 25% tristearin diet was supplemented with 5% triolein.

The type of dietary fat apparently exerts an inhibitory effect on calcium metabolism when calcium intake is low (<0.4% of the diet by weight). Nordin (1961) reported reduced absorption and retention of ^{47}Ca in rats receiving diets containing 20% tripalmitin or tristearin in comparison to a similar amount of triolein or tributyrin.

The significance of soap formation in the inhibition of calcium absorption has also been studied

in rats (Gacs and Barltrop, 1977). Soaps made with ^{47}Ca and fatty acids were introduced into the duodenum of rats and the absorption was measured after 4 hr by using a whole-body counter. The absorption of calcium was inversely correlated with the chain length of the fatty acid, varying from 1% for calcium stearate to 60% for calcium hexanoate. Increasing the degree of unsaturation of the fatty acid was accompanied by increased calcium absorption. The degree of calcium-soap formation and the inhibition of calcium absorption were well correlated ($r = 0.82$, $P < .001$). No soap formation was noted when fats were given in the form of triglycerides.

Kaup et al. (1990) used a factorial design to examine the effect of short- and long-term ingestion of dietary calcium (0.25 and 1.0%) and butterfat (5 and 20%) in rats. Calcium absorption decreased as the rats aged from 2 to 8 months. Increased butterfat ingestion had no effect on apparent calcium absorption among young rats but decreased it in mature rats. Ingestion of 1%, as compared to 0.25%, dietary calcium reduced the apparent absorption of calcium of young and mature rats.

Studies in laboratory rats, although not conclusive, indicate two trends. Calcium absorption and utilization are impaired when fat intakes exceed 10% of the energy intake. Saturated fatty acids or triglycerides made up of saturated fatty acids reduce calcium utilization.

Human Studies

Early studies in children consuming a mixed diet indicated a positive relationship between fat intake and apparent calcium absorption. Holt, et al. (1920) reported calcium absorption of 40.4% when the intake exceeded 30 mg calcium/kg body weight, but when the intake was less, the absorption averaged only 20.3%. The greatest absorption of calcium occurred when the dietary fat intake exceeded 3 g/kg body weight and when there was an adequate intake of 300–500 mg calcium/kg body weight. The principal source of dietary fat was milk and butter. The excretion of calcium in stools was not related to the excretion of total fat but showed a minor relation to the excretion of fat as a soap. Holt and Fales (1923) subsequently studied seven children aged 2–6 years who were fed diets containing fat at two levels (high fat: 30–65 g/day and low fat: 5–8 g/day) with a constant calcium intake (1.7–1.9 g/day). Calcium absorption was markedly reduced when the low-fat diet was consumed. The composition of the high-fat diet was mostly saturated fat and the low-fat diet was principally unsaturated fat. Impaired calcium absorption was associated with the increased presence of calcium soaps in the stool.

Other studies in humans indicate that dietary fat has no significant effect on calcium absorption or utilization. Mallon et al. (1930) studied the calcium retention of two college-aged women consuming 450–500 mg calcium/day who were fed high- and low-fat diets based on milk products for 18 days. They found no significant change in the calcium balance or fecal calcium excretion during two consecutive 3-day balance periods, and they concluded that fat per se did not affect calcium retention. Aub, et al. (1937) observed that the addition of 200 g fat to the diet of two healthy adults resulted in no increase in calcium excretion. Steggerda and Mitchell (1951) observed no effect on the calcium balance or fecal losses of the calcium of milkfat (5–160 g/day) fed at 1–32% of daily energy intake to 13 men. Fuqua and Patton (1953) studied nine college-aged women who consumed diets containing 600 mg calcium and supplying 45, 91, and 135 g of fat (19, 39, and 58% energy as fat). Mean calcium balances were not significantly influenced by fat intake, but they were highly variable. In a study of 12 men, von Dokkum et al. (1983) reported no change in calcium retention with an increase in lineoleic acid from 4 to 16% of energy intake when total fat intake was constant at 42% of energy.

In contrast, Basu and Nath (1946) studied the mineral metabolism of four young men fed diets containing 187–512 mg calcium/day and in which fat was provided principally by mustard oil, coconut oil, groundnut oil, sesame oil, or butterfat. The control was a fat-free diet. The addition of each of the fats, except coconut oil, slightly decreased the excretion of fecal calcium. With coconut oil, there was an increase in the fecal calcium excretion.

It is unclear whether usual intakes of dietary fat independently affect calcium utilization in humans. Excessive intakes of fat or pathological conditions that result in steatorrhea can negatively influence human calcium utilization (Aub et al., 1937).

MAGNESIUM

Scientific interest in the interaction between dietary fat and magnesium has been minimal in contrast to that regarding fat and calcium. In fact, much of what has been reported about magnesium bioavailability relative to fat has been the beneficiary of research on calcium and fat interactions.

In a review of the early literature, Seelig (1964) concluded that the available evidence was insufficient to define the effect of fat on magnesium metabolism. More recent experimental data may improve our understanding of this relationship.

The effects of dietary triglycerides on magnesium metabolism in weanling rats were studied by Tadayyon and Lutwak (1969). Magnesium absorption was significantly correlated ($r = 0.43$; $P < .01$) with fat absorption. Animals receiving either a fat-free diet or 25% triolein excreted the least fecal magnesium. At 5% intake, triolein, tripalmitin, and tristearin had similar effects on magnesium absorption and resulted in higher absorption of magnesium than with 25% tripalmitin or tristearin. The magnesium content of the femur was highest in the groups fed 5 or 25% triolein and lowest in the group fed 25% tripalmitin.

Kaup et al. (1990) observed a variable effect of fat on magnesium absorption in young and mature rats. Magnesium absorption was consistently greater among young rats fed high-butterfat (20%) diets versus low-butterfat (5%) diets. Magnesium absorption, however, tended to be reduced among mature rats fed more fat.

In a study of young men (von Dokkum et al., 1983), the magnesium balance was not affected by increasing dietary linoleate from 4 to 16% of energy intake (total fat intake was constant at 42% of energy intake). Similarly, reducing total fat intake from 42 to 22% with a constant linoleate intake of 18% did not affect magnesium retention.

These findings are consistent with the conclusion of Seelig (1964) that there is little evidence to support a definite effect of dietary fat on magnesium absorption. Recent observations suggest that diets high (>20%) in saturated dietary fat tend to reduce magnesium absorption in mature animals.

COPPER AND ZINC

In contrast to macrominerals, such as calcium and magnesium, that are required in amounts of hundreds of milligrams per day, the daily human requirements for trace elements, such as copper, zinc, and iron, are estimated to be in amounts ranging from about 3 to much less than 20 mg (National Research Council, 1989). Factors affecting the bioavailability of these trace substances have been intensively studied (Halstead et al., 1974; Mason, 1979). However, the influences of absolute amounts or relative proportions of dietary protein, carbohydrate, and fat have received little attention. In particular, dietary fat has only recently come under investigation as a putative factor affecting copper and zinc utilization.

Animal Studies

The effects of dietary linoleic acid on the tissue status of zinc and copper was examined in adult Fisher-344 male rats (Koo and Ramlet, 1984). One group received a diet containing 4% hydrogenated coconut oil (about 0.8% linoleate) and the other received a diet containing 3.4% nonhydrogenated coconut oil plus 0.6% lineoleic acid. The linoleate contents of the diets were 0.8 and 2.5%, respectively. After 6 weeks, the high-linoleate diet resulted in a significant depression in serum zinc (23.7 vs 21.4 μmol/L) and a slight reduction in serum copper concentration (19.7 vs 20.5 μmol/L). Liver and tibia wet weights were similar between the groups. The higher linoleate diet was associated with a significantly depressed zinc content of the tibia (145 vs 156 μg/g wet weight) and copper content of the tibia (0.20 vs 0.33 μg/g wet weight). Zinc and copper contents of the liver were not significantly affected by linoleate intake.

The effects of the type of dietary fat (coconut or safflower oil; 10% by weight) on copper and zinc absorption and utilization were studied in weanling, male Sprague-Dawley rats fed semipurified

diets containing adequate amounts of copper and zinc (Lukaski et al., 1986). Absorption and retention were estimated by determination of the remaining radioactivity by whole-body counting after labeling each animal with ^{67}Cu and ^{65}Zn. The safflower oil–based diet was associated with a slightly depressed absorption and retention of copper (35 vs 39% and 10 vs 11 days) and zinc (79 vs 84% and 82 vs 85 days). Safflower oil marginally depressed hepatic copper content (10.9 vs 11.2 μg/g dry weight), but significantly decreased liver zinc (287 vs 381 μg/g dry weight).

Lynch and Strain (1989) also reported an effect of type of dietary fat on hepatic copper. They studied weanling, male Wistar rats fed diets containing 20% by weight of either coconut or safflower oil with two different copper contents (0.4 and 11 ppm) for 56 days. In the rats fed the adequate copper diets, the liver copper content was significantly less (7.5 vs 18.2 μg/g wet weight) when safflower oil was the fat source. Similarly, safflower oil significantly decreased hepatic copper in the rats fed the copper-deficient diet (7.5 vs 8.1 μg/g wet weight).

The findings of these animal studies indicate that consumption of a diet consisting of predominantly polyunsaturated fatty acids can depress zinc and copper status.

Human Studies

The influence of the type and amount of dietary fat on human trace element metabolism has not been intensively investigated. Three highly trained endurance cyclists lived on a metabolic unit and consumed diets made of conventional Western foods for 3 months (Lukaski et al., 1982). The diets, which were high (45–55%) in carbohydrate and saturated or polyunsaturated fat were presented in random order for about 28 days each. The effects of the type and amount of dietary fat were evaluated by the chemical balance technique. Zinc and copper balance data were expressed as the values of two consecutive 6-day balance periods at the end of each dietary period. Zinc retention was significantly affected by the type of dietary fat (Table 2). Although a small difference in average zinc intake occurred, probably the result of changes in food used to accommodate the required changes in carbohydrate and fat composition of the diets, the zinc balance was significantly decreased by polyunsaturated fat as compared to saturated fat or carbohydrate. Relative zinc losses in the feces were increased when polyun-

TABLE 2 Summary of Two 6-Day Balance Periods in Three Cyclists Consuming Diets High (45–55%) in Carbohydrate (CHO), Saturated Fat (SATF), and Polyunsaturated Fatty acid (PUFA)

		Feces		Urine		
Diet	Intake (mg)	mg	% intake	mg	% intake	Balance
			Zinc			
CHO	23.1 ± 0.9[a]	19.5 ± 1.0	85 ± 3	0.9 ± 0.2	4 ± 0.6	2.7 ± 0.7[a]
PUFA	25.8 ± 1.0[b]	24.4 ± 1.1	95 ± 4	0.8 ± 0.2	3 ± 0.5	0.6 ± 0.9[b]
SATF	27.3 ± 0.9[b]	20.5 ± 1.4	75 ± 3	0.9 ± 0.2	3 ± 0.6	5.8 ± 0.8[a]
			Copper			
CHO	2.8 ± 0.2[a]	2.7 ± 0.2	98 ± 12	0.1 ± 0.01	3 ± 0.2	−0.03 ± 0.3
PUFA	2.3 ± 0.2[b]	2.2 ± 0.1	99 ± 4	0.1 ± 0.01	4 ± 0.4	−0.06 ± 0.1
SATF	2.3 ± 0.2[b]	2.1 ± 0.2	94 ± 3	0.1 ± 0.01	4 ± 0.2	0.04 ± 0.1
			Iron			
CHO	44.2 ± 2.2	30.1 ± 1.2[a]	69 ± 4[a]	0.1 ± 0.01	0.2 ± 0.01	14.0 ± 2.6[a]
PUFA	39.7 ± 3.1	37.9 ± 1.3[b]	96 ± 6[b]	0.1 ± 0.01	0.3 ± 0.03	1.7 ± 2.8[b]
SATF	46.3 ± 2.4	33.3 ± 1.9[a]	72 ± 7[a]	0.1 ± 0.01	0.2 ± 0.02	13.0 ± 3.9[a]

Values are mean ± SE.

[a,b] Values with different superscripts in same column are different ($P < .05$).

Source: Adapted from Lukaski et al. (1982).

TABLE 3 Effects of Linoleate Intake on Zinc, Copper, and Iron Retention in Three Cyclists

Linoleate intake (g/day)	Zinc retention (mg/6 days)	Copper retention (mg/6 days)	Iron retention (mg/6 days)
≤13	4.3 ± 1.0	0.01 ± 0.1	13.5 ± 2.1
≥140	0.6 ± 0.7	−0.06 ± 0.09	1.8 ± 1.9
P =	.05	.75	.009

Values are mean ± SE.
Source: Adapted from Lukaski et al. (1982).

saturated fat was consumed. The difference of approximately 5 mg in zinc retention exceeds the difference of 1.5 mg in zinc intake. There was no significant effect of dietary fat on the copper excretion and balance. Interestingly, the copper balance was positive, although not different than 0, only when saturated fat was consumed.

Because of the differences in the calculated linoleate intake between the polyunsaturated and saturated fat diets, it was possible to evaluate zinc and copper balances relative to intake of this fatty acid. Table 3 shows the effects of high- and low-linoleate intakes on zinc and copper balances. Low daily intakes of linoleate (about 13 g or less) were associated with a significantly greater zinc balance than higher intakes (140 g or more). Zinc retention was inversely and significantly related ($r = -0.49$; $P < .05$) to linoleate intake. The copper balance was not affected by linoleate intake.

IRON

The importance of iron in maintaining health and optimizing biological function has been long recognized by nutritionists (Dallman, 1986). However, only recently has there been intensive research to extend our understanding of the dietary factors affecting the availability of iron for absorption and utilization (Bowering et al., 1976). The effects of micronutrient factors, such as other minerals, ascorbic acid, and phytic acid, have been studied in detail (Hallberg, 1981), but the influences of macronutrients, such as protein, carbohydrate, and fat, are less defined and understood.

Animal Studies

The importance of the interaction between dietary fat and iron was highlighted by Kaufman et al. (1958). In adult male rats, the liver iron concentration decreased significantly from 88.6 to 15.7 mg/100 g when dietary fat (lard) was reduced from 30 to 10% and protein (casein) was maintained at 10%. When the diet was supplemented with additional iron (2% as ferric citrate), the liver iron also increased when fat was high (88.6–113.5 mg/100 g) or low (15.7–22.5 mg/100 g). Thus, both fat and iron increased the hepatic iron content in iron-adequate rats.

Amine and Hegsted (1975) reported an effect of dietary fat on iron absorption. In one experiment, iron absorption was determined by using ^{59}Fe in adult, iron-deficient, female rats fed diets containing varying amounts of coconut or corn oil (Table 4). Diets high in fat apparently promoted iron retention. Iron absorption was greater in diets in which fat was supplied as coconut oil than those in which fat was provided as corn oil. The difference between the oils was greatest when fat in the diet was low.

The effect of changing the amount and type of dietary fat on iron absorption in weanling, male iron-deficient rats fed varying amounts of heme and nonheme iron was studied by Bowering et al. (1977). Changes in the fat content included an increase from 5 to 20% of the diet and an exchange of lard for corn oil. Increasing the fat content and changing to a more saturated fat source were associated with small but significant increases in iron absorption. The enhancing effect on iron absorption observed

Table 4 Effects of Dietary Fat on Nonheme Iron Absorption by Iron-Deficient Rats

Fat	%	% ^{59}Fe retained
Cocount oil	5	38 ± 3[a]
	15	39 ± 4[a]
	30	46 ± 3[b]
Corn oil	5	25 ± 2[c]
	15	40 ± 2[a,d]
	30	42 ± 2[e]

Values are mean ± SD.
[a–e] Values with different superscripts are significantly different.
Source: Adapted from Amine and Hegsted (1975).

with changing the type of dietary fat was observed only when ferrous sulfate, and not heme iron, was fed at a suboptimal (15 ppm) amount in comparison to adequate (25 or 350 ppm) amounts.

These findings led other investigators to use dietary fat as a factor to influence iron absorption in their experiments. For example, the development of iron deficiency was promoted by feeding diets high in polyunsaturated fat (Amine et al., 1976; Rao et al., 1983). Feeding fat-free or saturated fat diets has been used to inhibit the development of iron deficiency in animals and fowl (Rao, et al., 1980, 1983).

Factorially arranged studies were undertaken to examine the effects of dietary iron intake (10 or 35 ppm), fat intake (5 or 35%), and type of fat (safflower or coconut oil) on heme and nonheme iron absorption and other indices of iron status (Johnson, et al., 1987). Rats were made moderately anemic by feeding an iron-deficient diet and then were fed 1 of the 16 experimental diets. Iron absorption was determined by feeding an ^{59}Fe test meal and by determining the remaining radioactivity in each animal by using whole-body counting for the following 5 weeks. Unlike in humans, nonheme iron was better absorbed than heme iron regardless of other dietary factors. Both heme and nonheme iron absorption was greater when high (30%) rather than low (5%) dietary fat was fed. Rats fed both heme or nonheme iron had significantly greater hemoglobin, change in hemoglobin, and liver iron content when fed coconut oil compared to safflower oil. Rats fed nonheme iron had greater liver iron, but not hemoglobin or change in hemoglobin, when fed high rather than low dietary fat. Rats fed heme iron had greater hemoglobin, change in hemoglobin, and liver iron when fed the high-fat rather than the low-fat diet.

These findings strengthen the growing evidence that the amount of dietary fat and its degree of saturation can affect the utilization of dietary iron. In general, the findings indicate that increasing amounts of saturated fat enhance and increasing amounts of unsaturated fat inhibit dietary iron absorption and utilization in rodent models.

Human Studies

In a study of competitive male cyclists (Lukaski et al., 1982), the effects of the type and amount of fat on iron retention also were examined. Iron retention was significantly affected by the type of fat consumed (see Table 2), and it was either significantly decreased by polyunsaturated fat or enhanced by saturated fat. Based on the apparent increase in fecal iron excretion, unsaturated fat apparently impairs iron absorption. High intakes of linoleate were associated with a reduced iron retention (see

Table 3). The iron balance was inversely and significantly related ($r = 0.64$; $P < .004$) to linoleate intake.

Similar findings were reported by van Dokkum et al. (1983), who examined the effects of changing the total fat intake and the amount of dietary linoleic acid on the iron balance and blood biochemical indices of the iron status in 12 men who were fed experimental diets for 28-day periods. Increasing the total fat intake from 22 to 42% of energy did not affect the iron balance. However, increasing the linoleic acid intake from 4 to 16%, while the total fat intake remained at 42%, resulted in a significant decrease in iron retention from 3.3 to 2.3 mg. At the same time, hemoglobin concentrations declined slightly from 9.6 to 9.1 mmol/L and the hematocrit decreased from 48 to 46%.

Meat Factor

Another factor known to influence iron absorption is meat. It is well recognized that heme iron, found primarily in meat or muscle, is better absorbed by humans than is nonheme iron (Hallberg, 1981). Furthermore, meat or meat products facilitate nonheme iron absorption. Efforts to identify the factor or factors in meat that promote nonheme iron absorption have been extensive (Cook and Monsen, 1976; Hazell, et al., 1978; Bjorn-Rasmussen and Hallberg, 1979; Hallberg and Rossander, 1982; Layrisse et al., 1984). Some investigators concluded that the active factor in meat that promotes nonheme iron absorption is an amino acid, such as glycine or histidine, or small peptides, such as glutathione, but the effects of these and other components of meat on iron absorption have not always been consistent. In a recent review, Zhang et al. (1990) proposed that the "meat factor" must be a chemical compound which binds iron with an action or mechanism that is different than chelation with an amino acid or peptide.

A candidate for the role of the meat factor is a fat or fatty acid. Mahoney et al. (1980) reported a relationship between a fat effect and the meat effect on iron absorption. They demonstrated that animals fed beef fat, compared to turkey fat, corn oil, or pork fat, were most efficient at converting iron from turkey meat into hemoglobin. One of the principal differences between beef fat and the other fats used in their study is that beef fat contains about 19% stearic acid (18:0), which is 10 times more than the stearic acid content of corn oil, 3.0 times more than that of turkey fat, and 1.5 times more than in lard (Mahoney et al., 1980). The findings suggest that dietary stearic acid may be important in facilitating iron absorption.

Johnson, et al. (1992) investigated the effects of stearic acid on iron utilization in rats. Anemic, male rats were fed diets containing stearic acid plus safflower oil (22% stearate plus 2% safflower oil and 20% stearate plus 4% safflower oil) or safflower oil (24%) and low (10 ppm) or high (39 ppm) iron as ferrous sulfate. The repletion of hemoglobin, hematocrit, liver iron, and absorption of ^{59}Fe were assessed. Compared to safflower oil, stearic acid had a significant positive effect on the repletion of hemoglobin, hematocrit, and liver iron. The effect was greatest when dietary iron was low.

In another experiment (Lukaski, et al., 1992), rats were fed low dietary iron (10–11 ppm) and 24% safflower oil, 20% stearic acid plus 4% safflower oil, 3.2% stearic acid plus 20.8% safflower oil, or 20% beef tallow plus 4% safflower oil. The 20% beef tallow provided 3.2% stearic acid. Rats fed beef tallow had significantly greater hemoglobin (6.9 vs 5.6 g/L) and hematocrit (21.5 vs 18.1%) repletion than did rats fed safflower oil, although the degree of repletion was less than that observed in rats fed 20% stearic acid (8.2 g/L and 25.9%). There was no difference in iron repletion of rats fed 3.2% stearic acid and rats fed beef tallow. Thus, stearic acid apparently increases iron utilization in rats fed nonheme iron.

Another experiment was designed to distinguish between the effects of meat protein and meat fat on iron utilization (Lukaski et al., 1992). Anemic rats were fed diets low or adequate in iron with either casein or beef (prime rib or fat-extracted beef) as the protein source and safflower oil, tallow, or stearic acid as the fat source. Dietary iron was low or adequate. Animals fed diets with tallow or stearic acid had the highest circulating hemoglobin concentrations regardless of the amount of iron in the diet. Also, rats fed prime rib had reticulocyte counts three to five times greater than rats fed casein

or lean beef with safflower oil. These findings indicate that beef fat enhances the utilization of iron for hemoglobin and red blood cell production.

The effects of combinations of various proteins (lean beef, skim milk, and egg white) and fats (beef fat, milkfat, and partially hydrogenated vegetable fat) on iron absorption in iron-adequate weanling rats have been examined (Kapsokefalou and Miller, 1993). Whole-body retention of ^{59}Fe was similar for lean beef plus tallow as compared to lean beef plus vegetable shortening (78 vs 70%) but was significantly less with egg plus shortening (78 vs 57%). Overall, there was no effect of fat type within a specific protein group, but beef was a significantly better protein source for promoting iron absorption. The authors concluded that the fat source (e.g., tallow) played an important role in facilitating the ability of lean beef to promote nonheme iron absorption.

A novel method has been used to examine the effects of dietary fat on in vivo mucosal iron kinetics. This experimental approach uses two radioisotopes of iron to estimate in vivo iron absorption and plasma iron kinetics into tissues (Nathanson et al., 1984). In mature dogs made iron deficient by consumption of an iron-deficient diet and serial phlebotomy, stearic acid (20%) significantly increased iron absorption (50 vs 21%), hemoglobin (25 vs 6 g/L), and erythrocyte volume (83 vs 32 mL) regeneration (Lukaski et al., 1993). This beneficial effect of stearic acid was the result of a significantly increased rate of transfer of iron from the mucosal cell to the plasma. When beef tallow, a typical source of dietary stearic acid, was studied, it also was shown to promote iron absorption and utilization as compared to safflower oil (McLaren et al., 1993).

These experiments were repeated with reduced amounts of fat (10%). It was found that stearic acid and beef tallow similarly enhanced iron absorption and utilization in anemic dogs (McLaren et al., 1997). Therefore, these findings support the hypothesis that dietary stearic acid may be one of the chemical factors in meat that promotes nonheme iron absorption and utilization.

MECHANISMS OF INTERACTION

Factors affecting the availability and utilization of minerals can potentially interact with these nutrients at various sites, including the intestinal lumen and mucosa, during transport from the gut to the target organ and at the cell membrane. The actual or proposed site of the fat-mineral interaction probably varies and is dependent on the individual mineral.

Calcium and Magnesium

The interactions between fatty acids and calcium and magnesium are generally accepted to occur within the intestinal lumen where soaps are formed (Boyd et al., 1932). This soap formation results in insoluble complexes that are not absorbed but are excreted in the feces (Gacs and Barltrop, 1977). The consistent observation that fecal calcium and magnesium losses are related to fecal fat excretion suggest that soap formation is the principal interaction between fats and minerals.

Copper and Zinc

The interaction between these trace elements and fat has not been studied in detail. Experimental data in rats indicate that although absorption and retention of copper and zinc, determined by using radioisotopes, are not significantly influenced by the type of fat, tissue pools of these trace elements are decreased by polyunsaturated fat (Koo and Ramlet, 1984; Lukaski et al., 1986; Lynch and Strain, 1989). These findings suggest that dietary fat influences copper and zinc redistribution in the body.

Preliminary data from men indicate that retention of zinc is significantly reduced when a diet high in polyunsaturated fat is consumed (Lukaski et al., 1982). This impairment is related to the increased fecal excretion of zinc. These findings in animals and humans suggest that fats may act at either the intestinal lumen or the cell membrane to exert the observed effects.

Although intensively studied, little is known about the factors that regulate copper and zinc absorption (Cousins, 1985). Copper and zinc are taken up by brush-border membrane transport systems

at the mucosal cell. These systems are not well understood, but they are thought to involve a carrier-mediated transport protein. Whether dietary fat directly affects the structure and function of these transport systems is not known. However, it is generally accepted that changes in dietary fat intake can significantly influence membrane fluidity, and thereby significantly affect cellular functions, including carrier-mediated transport and membrane-bound enzyme activities (Spector and Yorek, 1985).

Iron

Despite increasing evidence that dietary fat can influence iron absorption and retention (Lukaski et al., 1982; van Dokkum et al., 1983; Johnson et al., 1987; Johnson et al., 1992; Lukaski et al., 1993; McLaren et al., 1993), there is a paucity of information about the mechanism of this action. Saturated fat, particularly stearic acid, appears to promote iron uptake. Research involving chemical analyses of combustion products of tobacco smoke demonstrated that stearic acid has the capacity to effect the reduction of ferric to ferrous iron, to bind the resulting ferrous iron, and to transport the iron within the pulmonary macrophage (Qian and Eaton, 1989). Such enhancement of iron uptake by stearic acid may be related to the formation of stable monolayer stearate-iron films (Wheeler et al., 1971). Monolayer films of lipid anions may function as ionophores in the translocation of cations across biological membranes (Patel and Cornwell, 1977).

Fatty acids have been determined to participate in the uptake of iron at the mucosal membrane. Isolated brush-border membrane vesicles have been reported to have high concentrations of nonesterified fatty acids (Simpson and Peters, 1987a, 1987b). It was demonstrated by using an in vitro brush-border membrane preparation that the major iron-binding components were associated with free fatty acids, and that oleic and stearic acids show iron-binding capacities (Simpson and Peters 1987a, 1987b; Simpson, et al., 1988).

CONCLUSION

Experimental evidence in animals and humans indicates that dietary fat may be an important factor in mineral metabolism. The consensus is that dietary fat does significantly influence calcium and magnesium metabolism in healthy people with usual fat intakes, and there is accumulating evidence that fat may impact trace mineral metabolism.

Polyunsaturated fat may adversely affect the distribution of copper and zinc in animals. It apparently reduces the absorption of zinc in humans. Although the fecal excretion of zinc is increased with polyunsaturated fat, the mechanism of action is not known. It may involve alterations in the intestinal milieu that inhibit zinc-membrane receptor dynamics or changes in cellular membrane receptor function by altering membrane fluidity.

The most striking effect of dietary fat on trace mineral metabolism is the finding of the enhancement of iron uptake and utilization by saturated fat, specifically stearic acid. The effects are prominent when dietary iron is limiting, and they thus indicate a novel role in promoting an adequate iron status in humans. The practical importance of using stearic acid to facilitate iron absorption in humans is that it is has a minimal impact on serum cholesterol concentrations (Keys et al., 1965; Bonanome and Grundy, 1988) and it does not adversely effect platelet function and clotting (Schoene et al., 1993).

DIRECTIONS FOR FUTURE RESEARCH

Additional research is needed to delineate the mechanisms through which dietary fat and fatty acids affect trace mineral metabolism. It remains to be determined which intakes of fat and which fatty acids significantly change mineral absorption and utilization, and if this results in a significant accumulation of the minerals. The use of new experimental approaches, including cell culture techniques and cell biology tools, is recommended to further delineate physical and chemical interactions between fatty

acids and minerals at the cellular level. This information will be useful in the understanding of the factors that affect the bioavailability of minerals in the diet to optimize human health and function.

REFERENCES

Allen, L.H., and Solomons, N.W. (1984). Copper, in *Absorption and Malabsorption of Mineral Nutrients*, N.W. Solomons and I.H. Rosenberg, Eds., Liss, New York, pp. 199–229.

Amine, E.K., and Hegsted, D.M. (1975). Effect of dietary carbohydrates and fats on inorganic iron absorption, *J. Agric. Food Chem. 23*: 204–208.

Amine, E.K., Desilets, E.J., and Hegsted, D.M. (1976). Effect of dietary fats on lipogenesis in iron deficient anemic chicks and rats, *J. Nutr. 106*: 405–411.

Aub, J.C., Tibbetts, D.M., and McLean, R. (1937). The influence of parathyroid hormone, urea, sodium chloride, fat and of intestinal activity upon calcium balance, *J. Nutr. 13*: 635–655.

Basu, K.P., and Nath, H.P. (1946). The effect of different fats on calcium utilization of human beings, *J. Med. Res. 34*: 27–31.

Beadles, J.R., Mitchell, H.H., and Hamilton, T.S. (1951). The utilization of dietary calcium by growing albino rats fed diets containing lard or cocoa butter, *J. Nutr. 45*: 399–411.

Bjorn-Rasmussen, E., and Hallberg, L. (1979). Effect of animal proteins on the absorption of food iron in man, *Nutr. Metab. 23*: 192–202.

Bonanome, A., and Grundy, S.M. (1988) Effect of dietary stearic acid on plasma cholesterol and lipoprotein levels, *N. Engl. J. Med. 318*: 1244–1248.

Bowering, J., Sanchez, A.M., and Irwin, M.I. (1976). A conspectus of research on iron requirements of man, *J. Nutr. 106*: 985–1074.

Bowering, J., Masch, G.A., and Lewis, A.R. (1977). Enhancement of iron absorption in iron depleted rats by increasing dietary fat, *J. Nutr. 107*: 1687–1693.

Boyd, O.F., Crum, C.L., and Lyman, J.F. (1932). The absorption of calcium soaps and the relation of dietary fat to calcium utilization in the white rat, *J. Biol. Chem. 95*: 29–41.

Calverly, C.E., and Kennedy, C. (1949). The effect of fat on calcium and phosphorus metabolism of growing rats under a normal dietary regime, *J. Nutr. 38*: 165–175.

Cook, J.D., and Monsen, E.R. (1976). Food iron absorption in human subjects. III. Comparison of the effect of animal proteins on nonheme iron absorption, *Am. J. Clin. Nutr. 29*: 859–867.

Cousins, R.J. (1985). Absorption, transport, and hepatic metabolism of copper and zinc: special reference to metallothionein and ceruloplasmin, *Physiol. Rev. 65*: 238–309.

Dallman, P.R. (1986). Biochemical basis for the manifestations of iron deficiency, *Ann. Rev. Nutr. 6*: 13–40.

French, C.E., and Elliot, R.F. (1943). The interrelation of calcium and fat utilization, *J. Nutr. 25*: 17–21.

Fuqua, M.E., and Patton, M.B. (1953). Effect of three levels of fat intake on calcium metabolism, *J. Am. Diet. Assoc. 29*: 1010–1013.

Gacs, G., and Barltrop, D. (1977). Significance of calcium-soap formation for calcium absorption in the rat, *Gut 18*: 64–68.

Hallberg, L. (1981). Bioavailability of dietary iron in man, *Ann. Rev. Nutr. 1*: 123–140.

Hallberg, L., and Rossander, L. (1982). Absorption of iron from western-type lunch and dinner meals, *Am. J. Clin. Nutr. 35*: 502–509.

Halsted, J.A., Smith, J.C., and Irwin, M.I. (1974). A conspectus of research on zinc requirements of man, *J. Nutr. 104*: 345–378.

Hazell, T., Ledward, D.A., and Neale, R.J. (1978). Iron bioavailability from meat, *Br. J. Nutr. 39*: 631–638.

Holt, L.E., and Fales, H.L. (1923). Calcium absorption in children on a diet low in fat, *Am. J. Dis. Child. 25*: 247–256.

Holt, L.E., Courtney, A.M., and Fales, H.L. (1920). Calcium metabolism of infants and young children and the relation of calcium to fat excretion in the stools, *Am. J. Dis. Child. 19*: 201–222.

Irwin, M.I., and Kienholz, E.W. (1973). A conspectus of research on calcium requirements of man, *J. Nutr. 103*: 1019–1095.

Johnson, P.E. (1989a). Zinc absorption and excretion in humans and animals, in *Copper and Zinc in Inflammation*, R. Milanino, K.D. Rainsford, and G.P. Velo, Eds., Kluwer, Boston, pp. 103–131.

Johnson, P.E. (1989b). Factors affecting copper absorption in humans and animals, in *Copper Bioavailability and Metabolism* (*Advances in Experimental Biology and Medicine*, Vol. 258), C. Kies, Ed., Plenum, New York, pp. 71–80.

Johnson, P.E., Lukaski, H.C., and Bowman, T.D. (1987). Effects of level and saturation of fat and iron level and type in the diet on iron absorption and utilization by the rat, *J. Nutr. 117*: 501–507.

Johnson, P.E., Lukaski, H.C., and Korynta, E.D. (1992). The effects of stearic acid and beef tallow on iron utilization by the rat, *Proc. Soc. Exp. Biol. Med. 200*: 480–486.

Jones, H. (1940). The influence of fat on calcium and phosphorus metabolism, *J. Nutr. 20*: 367–375.

Kane, G.G., Lovelace, F.E., and McCay, C.M. (1949). Dietary fat and calcium wastage in old age, *J. Gerontol. 4*: 185–192.

Kapsokefalou, M., and Miller, D.D. (1993). Lean beef and beef fat interact to enhance nonheme iron absorption in rats., *J. Nutr. 123*: 1429–1434.

Kaufman, N., Klavins, J.V., and Kinney, T.D. (1958). Excessive iron absorption in rats fed low protein, high fat diets. *Lab. Invest. 7*: 369–376.

Kaup, S.M., Behling, A.R., Choquette, L., and Greger, J.L. (1990). Calcium and magnesium utilization in rats: effect of dietary butterfat and calcium and of age, *J. Nutr. 120*: 266–273.

Keys, A., Anderson, J.T., and Grande, F. (1965). Serum cholesterol response to changes in the diet. IV. Particular saturated fatty acids in the diet, *Metabolism 14*: 776–787.

Knudson, A., and Floody, R.J. (1940). Fat as a factor in the healing of rickets with vitamin D, *J. Nutr. 20*: 317–324.

Koo, S.I., and Ramlet, J.S. (1984). Effect of dietary linoleic acid on the tissue levels of zinc and copper, and serum high density lipoprotein cholesterol, *Atherosclerosis 50*: 123–132.

Latunde-Dada, G.O., and Neale, K.J. (1986). Review: availability of iron from foods, *J. Food Technol. 21*: 255–268.

Layrisse, J., Martinez-Torres, C., Leets, I., Taylor, P., and Ramirez, J. (1984). Effect of histidine, cysteine, glutathione, or beef on iron absorption in humans, *J. Nutr. 114*: 217–223.

Life Sciences Research Office, Federation of American Societies for Experimental Biology (1989). *Nutrition Monitoring in the United States—An Update Report on Nutrition Monitoring*, prepared for the U.S. Department of Agriculture and the U.S. Department of Health and Human Services, DHHS Publ. No. (PHS) 89-1255, Public Health Service, U.S. Government Printing Office, Washington, DC, pp. II–42–43.

Lukaski, H.C., Klevay, L.M., Bolonchuck, W.W., Mahalko, J.R., Milne, D.B., Johnson, L.K., and Sandstead, H.H. (1982). Influence of dietary lipids on iron, zinc and copper retention in athletes, *Fed. Proc. 41*: 275.

Lukaski, H.C., Lykken, G.I., and Klevay, L.M. (1986). Simultaneous determination of copper, iron and zinc absorption using gamma ray spectrospcopy: fat effects, *Nutr. Rep. Int. 33*: 139–146.

Lukaski, H.C., Johnson P.E., and Korynta, E.D. (1992). Beneficial effects of stearic acid on non-heme iron utilization in rats. *FASEB J. 6*: A1086.

Lukaski, H.C., McLaren, G.D., Johnson, P.E., and Smith, M.H. (1993). Enhanced intestinal iron absorption by dietary stearic acid: effect on mucosal iron kinetics, *FASEB J. 7*: A273.

Lynch, S.M. (1984). Iron, in *Absorption and Malabsorption of Mineral Nutrients*, N.W. Solomons and I.H. Rosenberg, Eds., Liss, New York, pp. 89–124.

Lynch, S.M., and Strain, J.J. (1989). Dietary saturated fat or polyunsaturated fat and copper deficiency in the rat, *Biol. Trace Elem. Res. 22*: 131–139.

McDoughall, E.J. (1938). The counteraction by fat of the anticalcifying action of cereals, *Biochem. J. 32*: 194–202.

Mahoney, A.W., Farmer, B.R., and Hendricks, D.G. (1980). Effects of level and source of dietary fat on the bioavailability of iron from turkey meat for the anemic rat, *J. Nutr. 110*: 1703–1708.

Mallon, M.G., Jordan, R., and Johnson, J. (1930). A note on the calcium retention of high and low fat diet, *J. Biol. Chem. 88*: 163–167.

Martell, A.E., and Smith, R.M. (1982). *Critical Stability Constants*, Vol. 5, First Suppl., Plenum, New York, p. 284.

Mason, K.E. (1979). A conspectus of research on copper metabolism and requirements of man, *J. Nutr. 109*: 1979–2066.

McLaren, G.D., Lukaski, H.C., Johnson, P.E., and Smith, M.H. (1993). Enhancement of intestinal iron absorption by dietary beef tallow and effect on mucosal iron kinetics in beagles. *Clin. Res. 41*: 688A.

McLaren G.D., Lukaski, H.C., Johnson, P.E., Misek, A.R., and Smith, M.H. (1997). Evidence for enhancement of nonheme iron absorption in beagle dogs by typical dietary levels of stearic acid in beef tallow. *Blood 90*(Suppl 1): 176.

Nathanson, M.H., McLaren, G.D., and Saidel, G.M. (1984). A model of intestinal absorption and plasma iron kinetics: optimal parameter estimates for normal dogs. *Comp. Biomed. Res. 17*: 55–70.

National Research Council (1989). *Recommended Dietary Allowances*, National Academy Press, Washington, DC, p. 284.

Nordin, B.C.E. (1968). Measurement and meaning of calcium absorption, *Gastroenterology 54*: 294–301.

Patel, G.S., and Cornwell, D.G. (1977). Surface phase separation and collapse of the stearate-alkaline earth cation complex, *J. Lipid Res. 18*: 1–5.

Perrin, D.P. (1979). *Stability Constants of Metal-Ion Complexes*, Part B, *Organic Ligands*, International Union of Pure and Applied Chemistry Chemical Data Series no. 22, Pergamon, Oxford, England, pp. 9–45.

Qian, M., and Eaton, J.W. (1989). Tobacco-borne siderophoric activity, *Arch. Biochem. Biophys. 275*: 280–288.

Rao, G.A., Manix, M., and Larkin, E.C. (1980). Reduction of essential fatty acid deficiency in rats fed a low iron fat free diet, *Lipids 15*: 55–60.

Rao, G.A., Crane, R.T., and Larkin, E.C. (1983). Reduction of hepatic steroyl-CoA desaturase activity in rats fed iron-deficient diets, *Lipids 18*: 537–575.

Rosenberg, I.R., and Solomons, N.W. (1984). Physiological and pathophysiological mechanisms in mineral absorption, in *Absorption and Malabsorption of Mineral Nutrients*, N.W. Solomons and I.H. Rosenberg, Eds., Liss, New York, pp. 1–13.

Schoene, N.W., Altman, M.A., Dougherty, R.M., Denver, E., and Aachen, J.M. (1993). Diverse effects of dietary stearic and palmitic acids on platelet morphology, in *Essential Fatty Acids and Eicosanoids*, A. Sinclair and R. Gibson, Eds., American Oil Chemists' Society, Champaign, IL, pp. 290–293.

Seelig, M.S. (1964). The requirement of magnesium by the normal adult. Summary and analysis of published data, *Am. J. Clin. Nutr. 14*: 342–390.

Sillen, L.G., and Martell, A.E. (1964). *Stability Constants of Metal-Ion Complexes*, Spec. Publ. No. 17, Chemical Society, London, p. 357.

Simpson, R.J., and Peters, T.J. (1987a). Iron-binding lipids of rabbit duodenal brush-border membrane, *Biochem. Biophys. Acta 898*: 181–186.

Simpson, R.J., and Peters, T.J. (1987b). Transport of Fe^{2+} across lipid bilayers: possible role of free fatty acids, *Biochem. Biophys. Acta 898*: 187–195.

Simpson, R.J., Moore, R., and Peters, T.J. (1988). Significance of nonestrified fatty acids in iron uptake by intestinal brush-border membrane vesicles, *Biochim. Biophys. Acta 941*: 39–47.

Smith, M.C., and Spector, H. (1940). Calcium and phosphorus metabolism in rats and dogs as influenced by the ingestion of mineral oil, *J. Nutr. 20*: 19–26.

Solomons, N.W. (1982). Biological availability of zinc in humans, *Am. J. Clin. Nutr. 35*: 1048–1075.

Solomons, N.W., and Cousins, R.J. (1984). Zinc, in *Absorption and Malabsorption of Mineral Nutrients*, N.W. Solomons and I.H. Rosenberg, Eds., Liss, New York, pp. 125–197.

Solomons, N.W., and Rosenberg, I.H. (1984). *Absorption and Malabsorption of Mineral Nutrients*, Liss, New York, pp. 1–295.

Spector, A.A., and Yorek, M.A. (1985). Membrane lipid composition and cellular function, *J. Lipid Res. 26*: 1015–1035.

Steggerda, F.R., and Mitchell, H.H. (1951). The calcium balance of adult human subjects on high- and low-fat (butter) diets, *J. Nutr. 45*: 201–211.

Stephen, A.M., and Wald, N.J. (1990). Trends in individual consumption of dietary fat in the United States, 1920–1984, *Am. J. Clin. Nutr. 52*: 457–469.

Swell, L., Trout, C.E., Field, H., and Treadwell, C.R. (1956). Effect of dietary fat and fatty acid on fecal excretion of a calcium oleate phosphate complex, *Proc. Soc. Exp. Biol. Med. 92*: 613–630.

Tadayyon, B., and Lutwak, L. (1969). Interrelationship of triglycerides with calcium, magnesium and phosphorus in the rat, *J. Nutr. 97*: 246–254.

von Dokkum, W., Cloughley, F.A., Hulsof, K.F.A.M., and Osterveen, L.A.M. (1983). Effect of variations in fat and linoleic acid intake on the calcium, magnesium and iron balance of young men, *Ann. Nutr. Metab., 27*: 361–369.

Wheeler, D.H., Potente, D., and Wittcoff, H. (1971). Adsorption of dimer, trimer, stearic, oleic, linoleic, nonanoic and azelaic acids on ferric oxide, *J. Am. Oil Chemists' Soc. 48*: 125–128.

Zhang, D., Carpenter, C.E., and Mahoney, A.W. (1990). A mechanistic hypothesis for meat enhancement of nonheme iron absorption: stimulation of gastric secretions and iron chelation, *Nutr. Res. 10*: 929–935.

FATTY ACIDS IN FOODS AND THEIR HEALTH IMPLICATIONS

SECOND EDITION, REVISED AND EXPANDED

EDITED BY

CHING KUANG CHOW

University of Kentucky
Lexington, Kentucky

MARCEL DEKKER, INC. NEW YORK • BASEL

www.dekker.com